

# Thumb and finger forces produced by motor units in the long flexor of the human thumb

W. S. Yu<sup>1</sup>, S. L. Kilbreath<sup>2</sup>, R. C. Fitzpatrick<sup>1</sup> and S. C. Gandevia<sup>1</sup>

<sup>1</sup>Prince of Wales Medical Research Institute, and University of New South Wales, Randwick 2031, Australia

<sup>2</sup>School of Physiotherapy, University of Sydney, Australia

The uncommonly good proprioceptive performance of the long flexor of the thumb, flexor pollicis longus (FPL), may add significantly to human manual dexterity. We investigated the forces produced by FPL single motor units during a weak static grip involving all digits by spike-triggered averaging from single motor units, and by averaging from twitches produced by intramuscular stimulation. Nine adult subjects were studied. The forces produced at each digit were used to assess how forces produced in FPL are distributed to the fingers. Most FPL motor units produced very low forces on the thumb and were positively correlated with the muscle force at recruitment. Activity in FPL motor units commonly loaded the index finger (42/55 units), but less commonly the other fingers ( $P < 0.001$ ). On average, these motor units produced small but significant loading forces on the index finger ( $\sim 5.3\%$  of their force on the thumb) with the same time-to-peak force as the thumb ( $\sim 50$  ms), but had no significant effect on other fingers. However, intramuscular stimulation within FPL did not produce significant forces in any finger. Coherence at 2–10 Hz between the thumb and index finger force was twice that for the other finger forces and the coherence to the non-index fingers was not altered when the index finger did not participate in the grasp. These results indicate that, within the long-term coordinated forces of all digits during grasping, FPL motor units generate forces highly focused on the thumb with minimal peripheral transfer to the fingers and that there is a small but inflexible neural coupling to the flexors of the index finger.

(Received 1 May 2007; accepted after revision 16 July 2007; first published online 26 July 2007)

**Corresponding author** S. Gandevia: Prince of Wales Medical Research Institute, Easy Street, Randwick, New South Wales 2031, Australia. Email: s.gandevia@unsw.edu.au

The human thumb has exceptional dexterity, especially for highly skilled tasks requiring precision grip between the thumb and various fingers (Napier, 1962). Flexion of the fingers is controlled by two extrinsic muscles, flexor digitorum profundus (FDP) and flexor digitorum superficialis, each compartmentalized for the individual fingers. By contrast, the human thumb has an anatomically distinct extrinsic muscle for its flexion. The flexor pollicis longus (FPL) muscle, which is not present in non-human primates, is the only muscle that can independently flex the distal phalanx of the thumb (Straus, 1942; Wood Jones, 1949; Landsmeer, 1986; Serlin & Schieber, 1993).

Compared with the fingers, proprioceptive performance involving the thumb is unexpectedly good. Passive movements are more accurately detected at the distal joint of the thumb than at the fingers (Refshauge *et al.* 1998). Force estimation is more accurate using FPL and thumb flexion than using FDP and finger flexion and this accuracy is maintained, contrary to predictions from Weber's law, even at extremely low forces (Kilbreath & Gandevia, 1993). The unique muscular control of the

thumb suggests that proprioceptive sense arising from FPL is the likely explanation for this improved performance. A large proportion of low-force motor units in FPL compared with FDP could explain this, but no data on the fundamental properties of FPL motor units are available.

Most daily use of the hand is for grasping (Schieber & Santello, 2004). As well as a high level of proprioceptive and tactile sensibility, grasping requires both independent and linked control of the thumb and finger flexors (e.g. Westling & Johansson, 1984; Edin *et al.* 1992). Independent force production by the digits may be limited, peripherally, by mechanical coupling between extrinsic muscles and, centrally, by linked neural output from motoneuronal pools (Kilbreath & Gandevia, 1994; Burstedt *et al.* 1997; Lang & Schieber, 2004; Schieber & Santello, 2004). Mechanical coupling can be due to passive connections between tendons. For example, the FPL tendon commonly attaches to the FDP tendons (Leijnse *et al.* 1997). Muscle shortening can also transmit forces via connective tissues to adjacent compartments and muscles through myofascial force transfer (Street, 1983;

Monti *et al.* 1999; Lieber & Friden, 2000; Huijing *et al.* 2003; Maas *et al.* 2003). Centrally, descending commands to the motoneurone pools limits digit independence (Kilbreath & Gandevia, 1994; Li & Harkness, 2004; Schieber & Santello, 2004). This central linkage has been revealed as common drive or short-term synchronization of motor units across muscles or compartments (Nordstrom *et al.* 1992; Reilly *et al.* 2004; Santello & Fuglevand, 2004; Winges & Santello, 2004; Hockensmith *et al.* 2005). For example, during grasping, FPL motor units showed higher short-term synchrony with those in the index compartment of FDP than with those in the other finger compartments (Winges & Santello, 2004), and motor unit activity in one FDP finger compartment commonly produced time-locked force changes at adjacent digits (Kilbreath *et al.* 2002).

We examined the properties of motor units in the uniquely human FPL and their significance for proprioceptive sense and independent control of the digits. To identify reasons for the increased proprioceptive sensibility of the thumb, the size distribution of FPL motor units was determined by spike-triggered averaging of FPL twitch forces and compared with data for FDP motor units obtained under similar conditions (Kilbreath *et al.* 2002). To identify force transfer from FPL motor units to the fingers, we sought finger tip forces during grasping that were time-locked to (i) voluntary firing of single FPL motor units and (ii) intramuscular stimulation of FPL motor units. A similar pattern in the two conditions

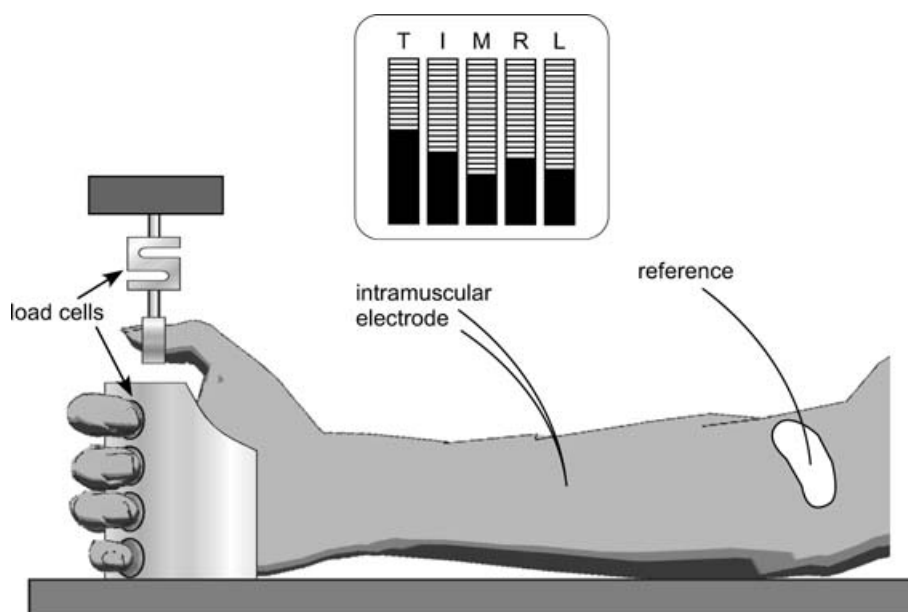
would suggest that peripheral intermuscular force transfer limited selective force production at the digits. To examine flexibility of force coupling between the thumb and the fingers that would indicate central independence, we examined the coherence between the forces exerted by the thumb and the fingers in grasp postures that included and excluded the index finger.

## Methods

Studies were conducted on the right hand of two female and seven male volunteer subjects, aged  $32.6 \pm 12.8$  years (mean  $\pm$  s.d), with a height of  $1.72 \pm 0.11$  m and weight of  $69.2 \pm 11.3$  kg. Three subjects were studied on more than one occasion. Prior to the experiment, informed written consent was obtained. The studies were conducted in accordance with the Declaration of Helsinki and the procedures were approved by the local human research ethics committee.

## Experimental design

The subject sat comfortably in a chair close to a table with the right forearm resting on a cushion. The right hand was positioned in mid-pronation so that it could gently grasp an instrumented cylinder. As it was fixed to a table, the task involved grasping but not lifting (Fig. 1). The



**Figure 1. Experimental set-up**

The distal pad of the thumb was positioned in a ring connected to a load cell which measured vertical force. There was an adjustable pillar just proximal to the distal interphalangeal joint of the thumb. Each finger pad was positioned over a load cell embedded in the cylinder to measure horizontal forces. Fine-wire intramuscular electrodes were inserted into flexor pollicis longus (FPL) to record from the single motor units. Feedback of force produced by each digit was available. T, thumb; I, index; M, middle; R, ring; L, little.

wrist was at  $\sim 30$  deg extension, the metacarpophalangeal joint was extended, and the forearm was at  $\sim 45$  deg to the coronal plane. The pad of the distal phalanx of the thumb was aligned horizontally in a ring connected to a load cell above, which measured vertical forces, while the proximal phalanx rested on a vertical pillar that was adjusted to ensure that the distal phalanx was horizontal. The pad of each finger was placed over load cells embedded in a cylinder 65 mm in diameter and 100 mm high. The embedded load cells, which measured forces normal to the surface, were positioned according to the average dimensions of 10 adult hands (Kilbreath *et al.* 2002). With this experimental arrangement, the thumb force was perpendicular to the forces exerted by the fingers and, because the cylinder was not lifted, it was not required that it oppose the finger forces.

Intramuscular electrodes were inserted using ultrasound guidance into FPL from the volar surface about 1–2 cm distal to the mid-point of the forearm (Fig. 1). The electrodes were composed of two strands of Teflon-coated stainless steel wire (75  $\mu\text{m}$  diameter), coiled and fused with ends cut at a sharp angle. The electrodes were threaded through a needle (23 gauge  $\times$  31 mm). After insertion, electrode position was confirmed by electromyographic (EMG) activity specific to flexion of the distal joint of the thumb and no activity with voluntary efforts involving adjacent muscles. This is an important criterion as similar electrodes inserted between adjacent muscles can record single motor unit activity from both (Hodges & Gandevia, 2000).

Subjects were instructed to grasp the cylinder with a weak but steady force. Auditory feedback of the EMG in FPL was provided along with visual feedback of force. A multi-channel light-emitting diode display showed force under the pad of the thumb and each of the fingers.

### Experimental protocols

In the first protocol, subjects grasped the cylinder and slowly increased the contraction force of thumb flexion until a single motor unit was clearly discriminated on a digital oscilloscope. The recruitment threshold for this 'test' unit, and for other units discriminated off-line, was determined from the force profiles of this initial series of grasps and a series of standardized ramp contractions in which force gradually increased from zero until the discharge of the unit. The background force at which the unit first discharged was recorded as the recruitment threshold. To collect data for spike-triggered averaging, subjects were asked to maintain the firing of the test motor unit with the aid of auditory feedback and the display of thumb force. During the recording period, subjects were reminded to maintain an even grasp with their fingers with the aid of the force feedback panel

whenever force under any finger fell or increased greatly. Data were collected from 55 motor units over 61–507 s (mean, 191 s). This yielded 525–4210 discharges for each spike-triggered average (mean, 1253). In one set of trials, subjects grasped the cylinder without using the index finger (i.e. thumb and digits 3–5 only) to determine how this affected forces in the other fingers.

In the second protocol, subjects grasped the cylinder as described in the first protocol. We stimulated cathodally through the intramuscular electrodes with a surface anode placed  $\sim 2$  cm away on the skin over the radius (Digitimer DS7). Stimulus intensity was initially set close to the level that evoked a very small local movement (pulse width, 50  $\mu\text{s}$ ), which was usually below sensory threshold. Recordings were usually collected at several intensities of stimulation. Stimulus frequency was low ( $\sim 1$  Hz), so that discrete force responses were identified. Data were collected for 18 stimulation sites for 72–425 s (mean, 275 s).

### Data acquisition and analysis

All data were recorded using Spike2 (CED 1401, Cambridge Electronic Design) and analysed off-line with customized software. The EMG signal was sampled at 16 kHz, amplified ( $\times 3000$ ) and band-pass filtered (60–3000 Hz with a 50 Hz notch). Force signals were sampled at 1 kHz. Initially, the single motor units were re-identified using templates and manual sorting. To determine the force fluctuations under each of the digits associated with the discharge of the single motor units, we removed the DC component of the force signals before performing spike-triggered averaging (e.g. Stein *et al.* 1972; Nordstrom *et al.* 1989). For each single unit recorded during a grasp, we measured the mean ( $\pm$  s.d.) baseline force for 10 ms prior to the discharge of the unit, the change from baseline to peak (or trough) force in the 100 ms after the trigger, and the latency of this peak. The latency was corrected for the delay between the motor unit spike and the trigger signal. A change from baseline to peak force in the spike-triggered response that consistently exceeded the pre-triggered force by more than two s.d. was regarded as significant. For the firing of each unit, we also computed the coefficient of variation based on the mean and s.d. of the interspike intervals. In the second protocol, a similar analysis of the background and evoked forces was performed when the trigger was the electrical stimulus, rather than the motor unit spike.

The effects of FPL motor unit activity *versus* stimulation on the digits were compared using one-way analyses of variance. The effects compared were the amplitude and the latency of the peak force. Planned contrasts were used to compare means from the thumb with the fingers separately. Similar comparisons examined means from

the index with the middle, ring and the little fingers separately. A  $\chi^2$  test was used to examine the frequency distribution of force changes under the digits (loading *versus* non-loading). Pearson correlation was used to examine the relationship between the twitch force of the motor unit and its recruitment threshold.

To compare the effect of grasping with and without the index finger, we used two-way analysis of variance. The effects compared were coherence values between the thumb force and that of the middle, ring and little finger, over the 2–10 Hz bandwidth. Statistical analyses were performed using SPSS (Chicago, IL, USA).

Coherence functions between force records (A and B) were calculated using a Spike2 script. We have previously published the complete computational algorithm (Fitzpatrick *et al.* 1996). Briefly, coherence (coh), was calculated as the squared modulus of the cross spectral density functions (csd) normalized by their power spectral density functions (psd).

$$\text{coh}(f) = (\Sigma \text{csd}_{AB}(f))^2 / [\Sigma \text{psd}_A(f) \times \Sigma \text{psd}_B(f)]$$

Parameters used for spectral calculations were a sampling frequency ( $f$ ) of 1 kHz, a sample length of 192 s with a 4-s data window, and a 12 Hz bandwidth with 0.25 Hz resolution. This yielded spectral estimates with normalized standard errors of 0.14.

## Results

### Properties of single FPL motor units

Activity was recorded from 55 single motor units in FPL while grasping a fixed cylinder. Most units were recruited at low force in a voluntary contraction. During the sustained contractions, units fired at a mean frequency of  $10.0 \pm 1.5$  Hz (range, 7.2–13.9 Hz) with a coefficient of variation of  $14.5 \pm 2.4\%$  (range, 9.7–19.4%). Spike-triggered averaging revealed that all units produced a detectable increment in force at the thumb pad. Two typical profiles of the averaged twitch forces on the thumb are shown on the left of Fig. 2 with the interspike interval histograms on the right. The mean time to the peak force for all the units was  $51 \pm 9$  ms. There was a strong correlation between the size of the motor unit twitch and the voluntary force at which the unit was recruited ( $r = 0.95$ ,  $P < 0.001$ ; Fig. 3A). The majority of units (34/55) had a twitch force below 10 mN, with a mean force of  $18.5 \pm 23.0$  mN (Fig. 3B, shaded bars). This skewed distribution of motor unit forces is very different from that of FDP motor units obtained under similar conditions (Fig. 3B, dashed lines; see Discussion).

### Distribution of FPL motor unit forces to the fingers

During grasping there were also significant force changes in the fingers time-locked to the discharge of single motor units in FPL. Based on spike-triggered averaging, the discharge of the FPL motor units was associated with a small net flexion force (1.0 mN) at the index finger (Fig. 4A). Across all motor units, the mean loading force on the index finger was 5.3% of the thumb loading force, which was significantly higher than that on the other fingers ( $P < 0.001$ ; Fig. 4B). Across all FPL motor units, there was a weak correlation between the forces produced in the thumb and the index finger ( $r = 0.39$ ,  $P < 0.01$ ).

The net change in force under each finger was the sum of forces from FPL units that produced loading of the finger, unloading, or no change in force. The distribution of force responses categorized in this way is shown in Fig. 4C. Activity in the FPL units usually loaded the index finger (42/55;  $P < 0.001$ ), whereas loading occurred less commonly for the other fingers. The time-to-peak force for the digits was  $\sim 50$  ms, and not significantly different between them.

### Intramuscular stimulation within FPL

Once the force distribution had been recorded during voluntary contractions, we usually delivered intramuscular stimulation at the sites from which single motor unit activity in FPL had been recorded ( $n = 18$  sites). The aim was to determine whether this produced significant intermuscular force transfer and loading of the index finger. As expected, a significant stimulus-evoked force was evoked from the thumb at each site (mean,  $10.3 \pm 9.6$  mN;  $P < 0.001$ ). An example is shown in Fig. 2A. No consistent pattern of loading was seen in the responses evoked in the fingers, although occasional unloading occurred (Fig. 2A). This contrasts with the loading forces seen in the index finger associated with voluntary FPL activity. Overall, a small loading force was produced consistently in the index finger by volitional activity within FPL, but not by a comparable intramuscular FPL stimulus.

### Coherence between thumb and finger forces during grasping

When attempting to maintain a constant grasp of the cylinder, significant fluctuations in force output of all five digits were seen across the 2–10 Hz bandwidth, which were maximal at 3–8 Hz (Fig. 5A). Typically, peaks of power were seen at specific frequencies that were not consistent between subjects. Between the thumb and each of the fingers, coherent force output was observed across the bandwidth and showed several tuned peaks at frequencies that were common for all fingers ( $\sim 3.5$ , 5.5 and 7 Hz; Fig. 5B). We measured the maximal coherence between

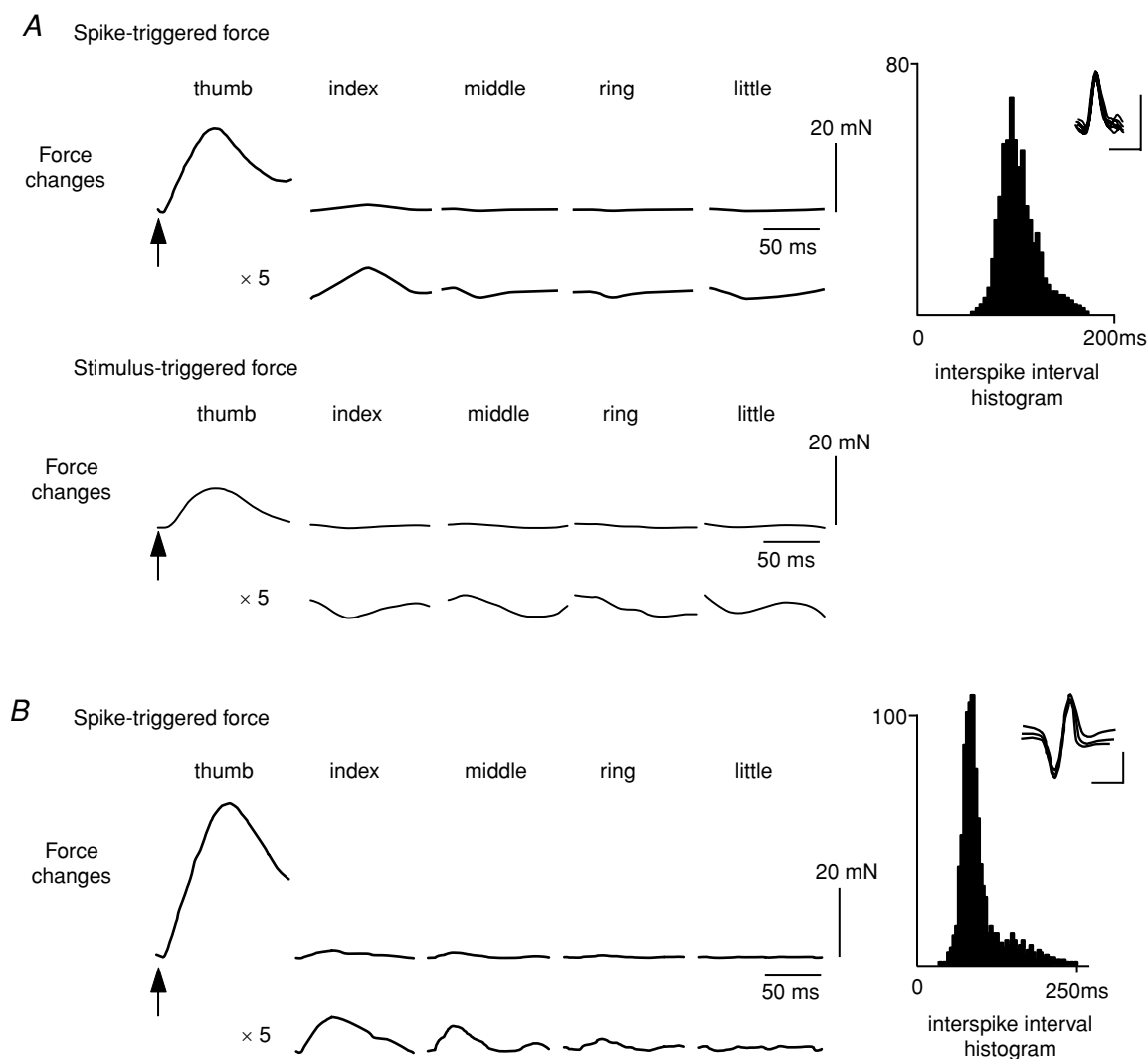
forces at the thumb and each of the fingers (e.g. open circles in Fig. 5B). Across all records, coherence between the thumb and the index finger was almost double that between the thumb and the other fingers at the frequency at which the thumb–index coherence peaked ( $P < 0.001$ ; Fig. 5C) and across the bandwidth (Fig. 6A).

To discover whether the pattern of coherent activity between the thumb and the fingers was fixed or modified in a task-dependent manner, coherence functions were determined for grasp in which the index finger was not used. In other words, we investigated whether the high

coherence of the index finger would be transferred to the middle finger. The coherence values for grasping without the index finger show that coherence levels between the thumb and the remaining fingers did not change significantly (Fig. 6B).

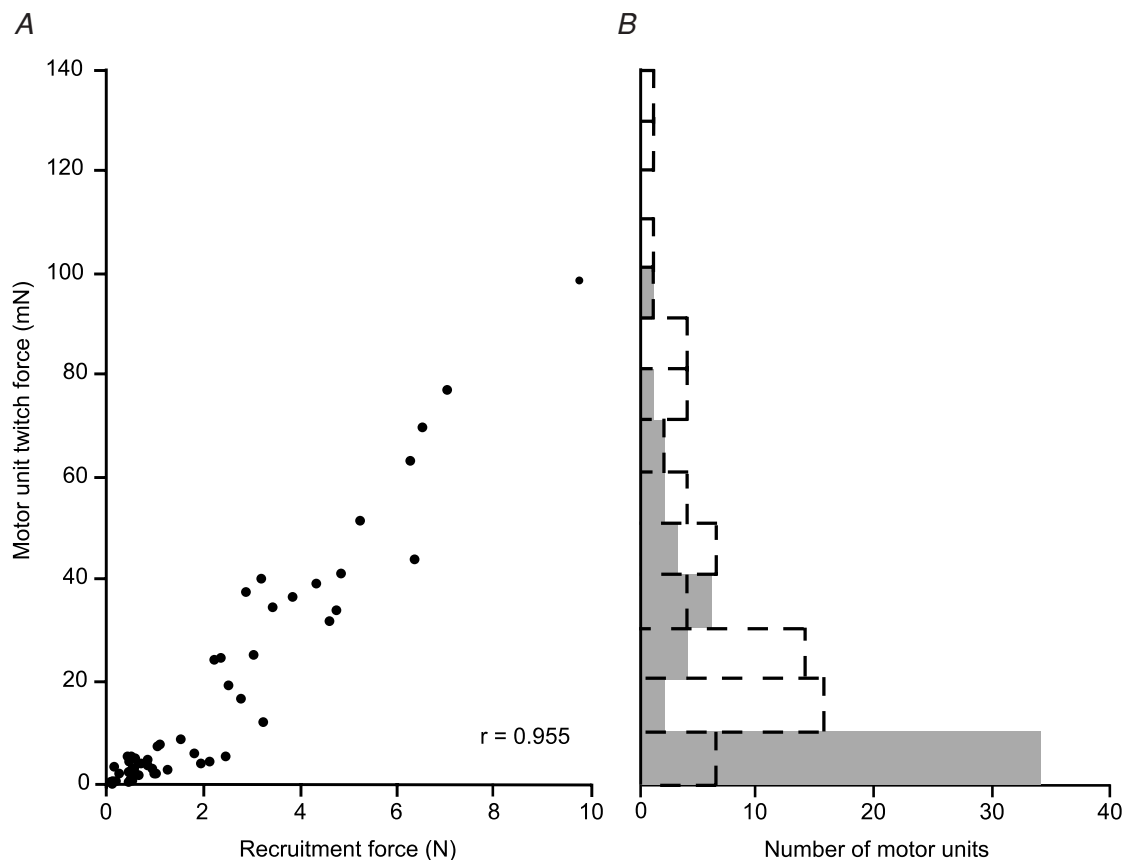
## Discussion

Although the human hand is highly dexterous, there are limits to the independent control of its digits. These constraints involve both central and peripheral



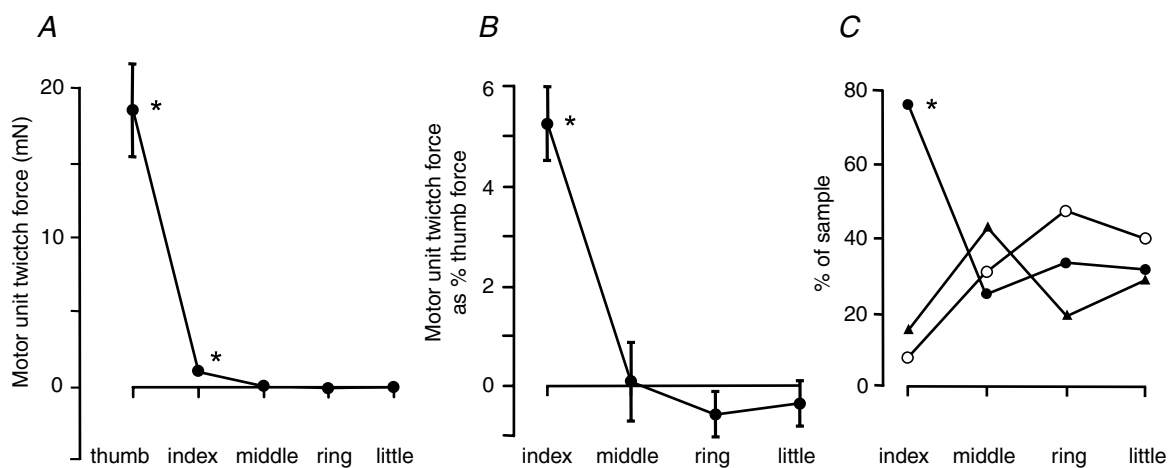
**Figure 2. Data obtained during grasping for two single motor units in flexor pollicis longus (FPL) and one site of intramuscular stimulation in FPL**

Left, the triggered averages of change in force under each digit are displayed. Right, for the single motor units, the interspike interval histograms are shown, and insets show the shape of the motor unit potential. The vertical arrow indicates the time of discharge of the unit or the time of intramuscular stimulation. The units in both A and B produced typical forces under the thumb and also significant loading of the index finger. There was a small unloading in the middle, ring and little fingers in A. There was loading in the first three fingers in B. A also shows an example of the average response to intramuscular stimulation at a site where motor unit activity was recorded. Unlike for the spike-triggered averages, there was unloading of the index finger. In both panels, axes for the inset represent 1 ms and 50  $\mu$ V.



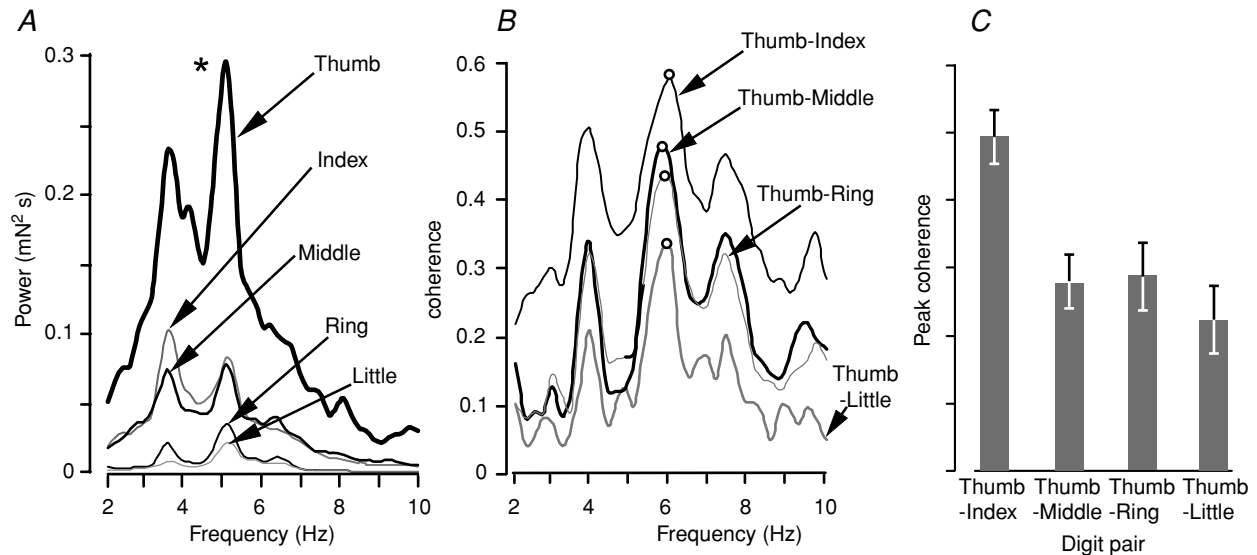
**Figure 3. Flexor pollicis longus (FPL) motor unit recruitment threshold and twitch force distribution**

A, relationship between the force at which a unit in FPL was recruited and the size of its twitch derived by spike-triggered averaging. Data are shown for 55 single motor units in FPL. The correlation between recruitment force and twitch force was statistically significant ( $P < 0.001$ ). B, distribution of the twitch forces of FPL single motor units during grasping. Data for 55 single motor units in FPL are shown as shaded bars. The majority of units in FPL produced small forces ( $< 10$  mN). Dashed line shows the distribution of the twitch forces produced by single motor units in flexor digitorum profundus (FDP) at the finger pads obtained in the study by Kilbreath *et al.* (2002).



**Figure 4. Twitch forces produced by flexor pollicis longus (FPL) motor units on each of the digits**

A and B, twitch force produced by single motor units in FPL during grasping (mean  $\pm$  s.e.m.). Apart from the primary loading on the thumb ( $P < 0.01$ ), there was significant loading on the index finger ( $P < 0.01$ ). Error bars for the fingers are smaller than the symbol size in A. This loading of the index is more clearly evident in B in which twitch forces are plotted relative to the loading on the thumb. C, percentage of units producing loading (●), unloading (○) and having no significant effect (▲) on the finger pads. Loading of the index finger occurred frequently and was less common for the other fingers (for all fingers,  $P < 0.001$ ). \*Significant changes.



**Figure 5. Power spectra of forces and coherences between the thumb and each finger**

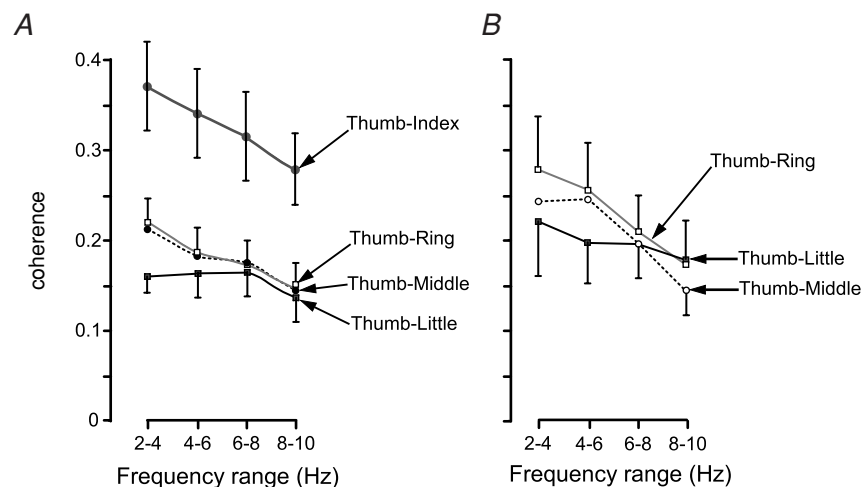
A, power spectra for each of the digits for one typical subject. The frequency 2–10 Hz bandwidth covered the main power in the force signal. B, coherence plots for the same subject between the thumb force and that of each finger show a similar pattern of common force output across all digits with several tuned peaks (o, peak coherence). C, mean peak coherence ( $n = 8$ , mean  $\pm$  S.E.M) between the thumb and index finger is approximately twice the value between the thumb and the other fingers.

mechanisms, including the voluntary ability to contract selectively the compartments of extrinsic muscles acting on the four digits. There are additional limits imposed by motor unit anatomy and tendon interconnections. This study provides new information about the neural control of the hand in grasping, and in particular about the actions of FPL.

The dexterity of the human thumb depends on FPL, the only muscle that flexes the distal phalanx. It is known that the capacity to judge forces exerted by FPL is unexpectedly

high compared with other hand muscles (Kilbreath & Gandevia, 1993); however, the responsible mechanisms have not been explored. This study showed that FPL has a large number of motor units that generate low twitch forces when compared with motor units in FDP (Fig. 3).

In a recent review, Enoka & Fuglevand (2001) calculated that there were 21 muscle fibres in the smallest motor unit (1 mN twitch force) in the first dorsal interosseous muscle (FDI). As follows, we have used a similar approach to estimate that there are  $\sim 15$  fibres for the same sized motor



**Figure 6. Coherence between the force of the thumb and each finger when grasping**

A, across the 2–10 Hz bandwidth, the thumb–index coherence was significantly greater than between the thumb and the other fingers. B, grasping without the index finger did not produce significantly different coherence results between the thumb and the remaining fingers. Data shown are mean  $\pm$  S.E.M. ( $n = 8$ ).

unit in FPL. For a motor unit with 1 mN twitch force, the tetanic force is 3.11 mN (Enoka & Fuglevand, 2001). If we assume that the ratio for moment arm adjustment is 1.89 (An *et al.* 1983), then the force in FPL is 5.87 mN. The mean cross-sectional area of a type I fibre is  $1893 \mu\text{m}^2$  in FDP (Polgar *et al.* 1973) and  $2140 \mu\text{m}^2$  in FDI (Dennett & Fry, 1988). Assuming that in FPL the cross-sectional area of the type I fibre is  $\sim 2000 \mu\text{m}^2$  and the specific tension is  $0.0002 \text{ mN } \mu\text{m}^{-2}$  (Enoka & Fuglevand, 2001), then the force exerted by a single fibre is 0.3786 mN, and the number of fibres innervated by this motor unit is  $\sim 15$ . This is lower than for FDI, but not as low as the five fibres estimated for the extraocular muscles using different methods (Feinstein *et al.* 1955).

When studied under the same conditions using spike-triggered averaging, motor units in FDP had a mean twitch force of  $\sim 50$  mN when assessed at a firing frequency of  $\sim 9$ – $10$  Hz. However, for FPL motor units, the mean twitch force was  $\sim 20$  mN when assessed at a similar firing frequency. Across the sample of FPL motor units, there was a strong correlation between the twitch force determined by spike-triggered averaging and the thumb force at which the motor unit was recruited. An orderly recruitment of units beginning with units of small absolute size allows production of finely graded force especially at low levels of effort (Henneman & Olson, 1965; Henneman *et al.* 1965; Henneman & Mendell, 1981; Gordon *et al.* 2004). Access to signals of peripheral force as well as signals of the motor command during such efforts presumably underpins the superior accuracy of the thumb in voluntary contractions.

Our study provides quantitative data on the distribution of FPL force to the fingers during a standard functional grasp of a cylinder in which the metacarpophalangeal joints were extended. During grasping, there was negligible force time-locked to the discharge of the single units in FPL under the pads of the middle, ring and little fingers. However, small, but significant, forces were recorded under the index finger, which were about  $\sim 5\%$  of the force exerted on the thumb. This distribution is likely to reflect, in part, an effect at the level of the output of motoneurone pools for two reasons. First, the time to the peak of the spike-triggered twitch force was the same for the force recorded at the thumb and the index finger. This would not be expected for intermuscular force transfer through a viscoelastic coupling (Hill, 1950; Partridge, 1966; Brown *et al.* 1982; Rack & Ross, 1984). This time-to-peak value ( $\sim 50$  ms) was within the range reported for long finger and thumb flexors using microstimulation (Fuglevand *et al.* 1999). However, it would be consistent with a degree of neural synchronization between motoneurons of FPL and motoneurons innervating the index compartment of FDP. Evidence from paired motor unit recordings indicates that short-term synchronization is higher between units in FPL and the index compartment of FDP than between FPL units and units innervating other parts of FDP (Winges

& Santello, 2004; Hockensmith *et al.* 2005; Winges *et al.* 2006). Second, this limited distribution of force from the thumb to index finger did not occur when microstimulation within FPL was used to generate small forces of a size within the range measured for FPL units. Hence, there was minimal transmission of force across to the fingers ( $< 6\%$ ). This result puts a relatively low upper limit on the force transfer between adjacent human muscles during a maintained static contraction (Monti *et al.* 2001; Huijing, 2003; Yucesoy *et al.* 2003, 2005; Smeulders *et al.* 2005; Meijer *et al.* 2006).

The results obtained with spike- and stimulus-triggered averaging of forces evoked under the finger pads point to a higher degree of neural coupling between the FPL and the index component of FDP than with its other components. The pattern of coherence between the forces at the digits, which shows greater coherence with the index finger, is consistent with this view. Across the bandwidth covering the observed force fluctuations during grasping, the coherences between the forces at the thumb and each of the fingers were relatively high (0.2–0.6) and greater than could be explained by the transfer of motor unit force from FPL seen here. It is likely that this reflects a coordinated common modulation of the cortical drive to the digits during grasping (e.g. Santello & Soechting, 2000; Baker *et al.* 2003; see also Semmler *et al.* 2004). However, the coherence of the thumb with the index force was higher than its force coherence with the other fingers (Winges *et al.* 2006). For the frequency at which the highest coherence was observed in each subject ( $\sim 3$ – $7$  Hz), the thumb–index coherence was, on average, 76% higher than the coherence of the thumb with the other fingers, and this may reflect short-term intermuscular force transfer. We cannot comment on coherence at frequencies beyond 10 Hz as power in the force signal beyond 10 Hz was small, but this warrants further study given the reported coherence between the firing of single motor units in a grasp (Johnston *et al.* 2005).

An interesting phenomenon occurred when the index finger was lifted slightly off the test object such that its net flexor force was zero. The coherence of the thumb with the non-index fingers did not change and the high coherence previously observed with the index was not ‘transferred’ to any other finger. One interpretation of this result is that part of the neural system linking the output of FPL and the index component of FDP may be ‘hard-wired’. One level at which this could occur is via the limited branching of corticospinal axons to drive more than one motor nucleus (Buys *et al.* 1986; Fetz & Cheney, 1987).

The present results delineate an important coupling in the behaviour of the long flexor of the thumb and index finger. They also provide quantitative data so that the ‘selectivity’ with which the thumb operates can be calculated. A selectivity index was introduced by Schieber (1991) to measure digital dexterity in the monkey. This



index can now be derived for motor units in FPL that are active in functional grasp, using the approach of Keen & Fuglevand (2003) for extensor digitorum, the primary finger extensor. Based on the results of our study, the selectivity index for FPL motor units is 0.95 (i.e.  $d/d_{\max}$ , where  $d = \sqrt{(\sum_{i=1-5} (\tau_i - 0.2)^2)}$ , where  $\tau_i$  is the force in digit  $i$ , and  $d_{\max} = 1.789$ ). By contrast, using the data of Kilbreath *et al.* (2002) obtained during similar grasping, we calculate that the index is 0.62, 0.46, 0.49 and 0.45 for motor units in FDP operating on the index, middle, ring and little fingers, respectively. This represents performance during volitional tasks, whereas the selectivity based on intramuscular microstimulation can be higher, as first shown for the finger extensors (Keen & Fuglevand, 2003, 2004) and confirmed here for the FPL.

## Conclusions

In evolutionary terms, FPL is an addition to the control system for human manual dexterity. This muscle has very fine proprioceptive control for grasping and our results suggest that this is possible because the muscle possesses a large population of motor units producing lower forces than occurs in the long flexor of the fingers (FDP). Furthermore, in tonic voluntary contractions, FPL can be activated selectively with minimal peripheral force transfer to the adjacent digits – a level of independence not seen during phasic movements (Kilbreath & Gandevia, 1994). The coherence analysis suggests that there is a strong source of coordinated common drive between FPL and all compartments of FDP, but most of this is not mediated through short-term synchronization.

## References

- An K, Ueba Y, Chao E, Cooney W & Linscheid R (1983). Tendon excursion and moment arm of index finger muscles. *J Biomech* **16**, 419–425.
- Baker SN, Pinches EM & Lemon RN (2003). Synchronization in monkey motor cortex during a precision grip task. II. Effect of oscillatory activity on corticospinal output. *J Neurophysiol* **89**, 1941–1953.
- Brown TI, Rack PM & Ross HF (1982). Forces generated at the thumb interphalangeal joint during imposed sinusoidal movements. *J Physiol* **332**, 69–85.
- Burstedt MK, Edin BB & Johansson RS (1997). Coordination of fingertip forces during human manipulation can emerge from independent neural networks controlling each engaged digit. *Exp Brain Res* **117**, 67–79.
- Buys EJ, Lemon RN, Mantel GW & Muir RB (1986). Selective facilitation of different hand muscles by single corticospinal neurones in the conscious monkey. *J Physiol* **381**, 529–549.
- Dennett X & Fry HJ (1988). Overuse syndrome: a muscle biopsy study. *Lancet* **1**, 905–908.
- Edin BB, Westling G & Johansson RS (1992). Independent control of human finger-tip forces at individual digits during precision lifting. *J Physiol* **450**, 547–564.
- Enoka RM & Fuglevand AJ (2001). Motor unit physiology: some unresolved issues. *Muscle Nerve* **24**, 4–17.
- Feinstein B, Lindegard B, Nyman E & Wohlfart G (1955). Morphologic studies of motor units in normal human muscles. *Acta Anat (Basel)* **23**, 127–142.
- Fetz EE & Cheney PD (1987). Functional relations between primate motor cortex cells and muscles: fixed and flexible. *Ciba Found Symp* **132**, 98–117.
- Fitzpatrick R, Burke D & Gandevia SC (1996). Loop gain of reflexes controlling human standing measured with the use of postural and vestibular disturbances. *J Neurophysiol* **76**, 3994–4008.
- Fuglevand AJ, Macefield VG & Bigland-Ritchie B (1999). Force-frequency and fatigue properties of motor units in muscles that control digits of the human hand. *J Neurophysiol* **81**, 1718–1729.
- Gordon T, Thomas C, Munson J & Stein R (2004). The resilience of the size principle in the organization of motor unit properties in normal and reinnervated adult skeletal muscles. *Can J Physiol Pharmacol* **82**, 645–661.
- Henneman E & Mendell L (1981). Functional organization of motoneuron pool and inputs. In *Handbook of Physiology*, section 1, *the Nervous System*, ed. Brooks V, pp. 423–507. Williams & Wilkins, Baltimore, MD.
- Henneman E & Olson CB (1965). Relations between structure and function in the design of skeletal muscles. *J Neurophysiol* **28**, 581–598.
- Henneman E, Somjen G & Carpenter DO (1965). Functional significance of cell size in spinal motoneurons. *J Neurophysiol* **28**, 560–580.
- Hill AV (1950). The series elastic component of muscle. *Proc R Soc Lond B Biol Sci* **137**, 273–280.
- Hockensmith GB, Lowell SY & Fuglevand AJ (2005). Common input across motor nuclei mediating precision grip in humans. *J Neurosci* **25**, 4560–4564.
- Hodges PW & Gandevia SC (2000). Pitfalls of intramuscular electromyographic recordings from the human costal diaphragm. *Clin Neurophysiol* **111**, 1420–1424.
- Huijing PA (2003). Muscular force transmission necessitates a multilevel integrative approach to the analysis of function of skeletal muscle. *Exerc Sport Sci Rev* **31**, 167–175.
- Huijing PA, Maas H & Baan GC (2003). Compartmental fasciotomy and isolating a muscle from neighboring muscles interfere with myofascial force transmission within the rat anterior crural compartment. *J Morphol* **256**, 306–321.
- Johnston JA, Winges SA & Santello M (2005). Periodic modulation of motor-unit activity in extrinsic hand muscles during multidigit grasping. *J Neurophysiol* **94**, 206–218.
- Keen DA & Fuglevand AJ (2003). Role of intertendinous connections in distribution of force in the human extensor digitorum muscle. *Muscle Nerve* **28**, 614–622.
- Keen DA & Fuglevand AJ (2004). Common input to motor neurons innervating the same and different compartments of the human extensor digitorum muscle. *J Neurophysiol* **91**, 57–62.
- Kilbreath SL & Gandevia SC (1993). Neural and biomechanical specializations of human thumb muscles revealed by matching weights and grasping objects. *J Physiol* **472**, 537–556.

- Kilbreath SL & Gandevia SC (1994). Limited independent flexion of the thumb and fingers in human subjects. *J Physiol* **479**, 487–497.
- Kilbreath SL, Gorman RB, Raymond J & Gandevia SC (2002). Distribution of the forces produced by motor unit activity in the human flexor digitorum profundus. *J Physiol* **543**, 289–296.
- Kilner JM, Alonso-Alonso M, Fisher R & Lemon RN (2002). Modulation of synchrony between single motor units during precision grip tasks in humans. *J Physiol* **541**, 937–948.
- Landsmeer JM (1986). A comparison of fingers and hand in varanus, opossum and primates. *Acta Morphol Neerl Scand* **24**, 193–221.
- Lang CE & Schieber MH (2004). Human finger independence: limitations due to passive mechanical coupling versus active neuromuscular control. *J Neurophysiol* **92**, 2802–2810.
- Leijnse JN, Walbeehm ET, Sonneveld GJ, Hovius SE & Kauer JM (1997). Connections between the tendons of the musculus flexor digitorum profundus involving the synovial sheaths in the carpal tunnel. *Acta Anat (Basel)* **160**, 112–122.
- Li ZM & Harkness DA (2004). Circumferential force production of the thumb. *Med Eng Physics* **26**, 663–670.
- Lieber RL & Friden J (2000). Functional and clinical significance of skeletal muscle architecture. *Muscle Nerve* **23**, 1647–1666.
- Maas H, Jaspers RT, Baan GC & Huijing PA (2003). Myofascial force transmission between a single muscle head and adjacent tissues: length effects of head III of rat EDL. *J Appl Physiol* **95**, 2004–2013.
- Meijer HJ, Baan GC & Huijing PA (2006). Myofascial force transmission is increasingly important at lower forces: firing frequency-related length-force characteristics of rat extensor digitorum longus. *Acta Physiol (Oxf)* **186**, 185–195.
- Monti RJ, Roy RR & Edgerton VR (2001). Role of motor unit structure in defining function. *Muscle Nerve* **24**, 848–866.
- Monti RJ, Roy RR, Hodgson JA & Edgerton VR (1999). Transmission of forces within mammalian skeletal muscles. *J Biomech* **32**, 371–380.
- Napier J (1962). The evolution of the hand. *Sci Am* **207**, 56–62.
- Nordstrom MA, Fuglevand AJ & Enoka RM (1992). Estimating the strength of common input to human motoneurons from the cross-correlogram. *J Physiol* **453**, 547–574.
- Nordstrom MA, Miles TS & Veale JL (1989). Effect of motor unit firing pattern on twitches obtained by spike-triggered averaging. *Muscle Nerve* **12**, 556–567.
- Partridge LD (1966). Signal-handling characteristics of load-moving skeletal muscle. *Am J Physiol* **210**, 1178–1191.
- Polgar J, Johnson MA, Weightman D & Appleton D (1973). Data on fibre size in thirty-six human muscles. An autopsy study. *J Neurol Sci* **19**, 307–318.
- Rack PM & Ross HF (1984). The tendon of flexor pollicis longus: its effects on the muscular control of force and position at the human thumb. *J Physiol* **351**, 99–110.
- Refshaug KM, Kilbreath SL & Gandevia SC (1998). Movement detection at the distal joint of the human thumb and fingers. *Exp Brain Res* **122**, 85–92.
- Reilly KT, Nordstrom MA & Schieber MH (2004). Short-term synchronization between motor units in different functional subdivisions of the human flexor digitorum profundus muscle. *J Neurophysiol* **92**, 734–742.
- Santello M & Fuglevand AJ (2004). Role of across-muscle motor unit synchrony for the coordination of forces. *Exp Brain Res* **159**, 501–508.
- Santello M & Soechting JF (2000). Force synergies for multifingered grasping. *Exp Brain Res* **133**, 457–467.
- Schieber MH (1991). Individuated finger movements of rhesus monkeys: a means of quantifying the independence of the digits. *J Neurophysiol* **65**, 1381–1391.
- Schieber MH & Santello M (2004). Hand function: peripheral and central constraints on performance. *J Appl Physiol* **96**, 2293–2300.
- Semmler JG, Sale MV, Meyer FG & Nordstrom MA (2004). Motor-unit coherence and its relation with synchrony are influenced by training. *J Neurophysiol* **92**, 3320–3331.
- Serlin DM & Schieber MH (1993). Morphologic regions of the multitendoned extrinsic finger muscles in the monkey forearm. *Acta Anat (Basel)* **146**, 255–266.
- Smeulders MJ, Kreulen M, Hage JJ, Huijing PA & van der Horst CM (2005). Spastic muscle properties are affected by length changes of adjacent structures. *Muscle Nerve* **32**, 208–215.
- Stein RB, French AS, Mannard A & Yemm R (1972). New methods for analysing motor function in man and animals. *Brain Res* **40**, 187–192.
- Straus W Jr (1942). Rudimentary digits in primates. *Q Rev Biol* **17**, 228–243.
- Street SF (1983). Lateral transmission of tension in frog myofibers: a myofibrillar network and transverse cytoskeletal connections are possible transmitters. *J Cell Physiol* **114**, 346–364.
- Westling G & Johansson RS (1984). Factors influencing the force control during precision grip. *Exp Brain Res* **53**, 277–284.
- Winges SA, Johnston JA & Santello M (2006). Muscle-pair specific distribution and grip-type modulation of neural common input to extrinsic digit flexors. *J Neurophysiol* **96**, 1258–1266.
- Winges SA & Santello M (2004). Common input to motor units of digit flexors during multi-digit grasping. *J Neurophysiol* **92**, 3210–3220.
- Wood Jones F (1949). *The Principles of Anatomy as Seen in the Hand*. Bailliere, Tindall and Cox, London.
- Yucesoy CA, Baan GC, Koopman BH, Grootenboer HJ & Huijing PA (2005). Pre-strained epimuscular connections cause muscular myofascial force transmission to affect properties of synergistic EHL and EDL muscles of the rat. *J Biomech Eng* **127**, 819–828.
- Yucesoy CA, Koopman BH, Baan GC, Grootenboer HJ & Huijing PA (2003). Effects of inter- and extramuscular myofascial force transmission on adjacent synergistic muscles: assessment by experiments and finite-element modeling. *J Biomech* **36**, 1797–1811.

## Acknowledgements

This study was supported by the National Health and Medical Research Council of Australia. We thank Dr Robert Gorman for expert technical assistance.